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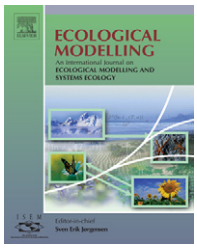

Review

The representation of allelopathy in ecosystem-level forest models

*Juan A. Blanco**

Department of Forest Sciences, Faculty of Forestry, The University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

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ABSTRACT

Allelopathy is one of the factors that determine interactions among plants. Allelochemicals have been found in many forest ecosystems, but the importance of allelopathy depends on forest type and environmental conditions. Despite the wide presence of this phenomenon, few forest models have incorporated a representation of allelopathy, but its inclusion should be considered in forest models dealing with environmental stress, exotic plant invasions and ecological succession. Multiple factors influence allelochemical production and toxicity, including nutrient availability, soil moisture and texture, solar radiation, and temperature. Ecosystem-level effects of allelopathy include changes in germination rates, inhibition of seedling growth, mycorrhizal function, insect and bacterial growth, inhibition of nitrification or litterfall decomposition and dieback of mature trees. To illustrate some potential consequences of incorporation some aspects of allelopathy, in an ecosystem-level model, a virtual experiment was carried out with the forest ecosystem-level model FORECAST. This revealed different effects of allelopathy on several ecological variables depending on the type of allelopathic influence simulated. In addition, this experiment showed the utility of ecosystem-level models to simulate, if not directly the allelopathic interactions, at least the ecological effects of allelopathy at the ecosystem level. Overall, my work points out that researchers and forest managers should think carefully about the need to include allelopathy as a way of improving the accuracy of forest models and ecosystem-based decision support tools.

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* Tel.: +1 604 822 2507/6018; fax: +1 604 822 9133.
E-mail address: juan.blanco@ubc.ca.
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1. Introduction

Models that represent forest development, from an ecosystem perspective, are proving to be the most suitable tools to assess the sustainability of forest practices. Although different types of forest models have been used for this purpose, hybrid models are possibly the most useful in forest management, because they combine the advantages of processes models and historical bioassay models to compensate for the shortcomings of both approaches (Kimmins, 2004). In order to study the biophysical consequences of forest management at an ecosystem level, a model should represent the most important components that integrate the forest ecosystem in question, independently of the level of complexity of such a model. Among these components, forest soil is the primary component influenced by silviculture practices, because it is an important nutrient and water reserve. Forest soil is a complex environment where multiple biogeochemical processes are superposed at the same time, and as a consequence many models only simulate soil processes through empirical growth modifiers, and therefore they cannot assess biophysical sustainability in ecosystems where moisture and nutrients play a key role in ecosystem sustainability. One of these processes is allelopathy, defined as the effects produced on growth and development of target plants caused by chemicals produced by donor plants (Rice, 1984). For some ecosystems the omission of allelopathy may act as a significant limitation on a model.

Historically, the study of allelopathic interactions has been focused mainly on relationships between crops and weeds (Pellissier and Souto, 1999), and recently, the chemistry and mode of action of allelochemicals has been studied (Einhellig, 2004). However, studies about allelopathic relationships in forest soils are still scarce and dispersed, possibly due to the difficulty of the separation of allelochemical effects from other factors, especially nutrient competition (Weidenhamer et al., 1989; Wardle et al., 1998). Nevertheless, several studies have identified the importance of allelopathy in forest ecosystems. For example, Rietveld et al. (1983) have reported premature birch (*Betula papyrifera* Marsh) death in mixed plantations with walnut (*Juglans nigra* L.). Problems of conifer regeneration caused by ericaceous understory species have also been described (Mallik, 2003). These examples show the importance of chemical interactions among plants in forest development and, therefore, show the necessity of including these relationships in forest models dealing with similar situations.

The first theoretical representation of allelopathic relationships was proposed by Maynard-Smith (1974), using a modified Lotka–Volterra competition model. Improvements and refinements of this model have been used to analyze allelopathy in plant communities and algae (Dubey and Hussain, 2000; Liu et al., 2003; Solé et al., 2005), and Einhellig and co-workers have developed conceptual models of about the mode of action of allelochemicals (see Einhellig (2004) for more references). Other contributions include theoretical models of allelopathy as a continuous time Markov process (Lanchier, 2004), separation of allelopathy from competition (Weidenhamer et al., 1989; Nakamaru and Iwasa, 2000), clarification of the ecophysiological foundations of allelopathy (An et al., 1993; Mukhopadhyay et al., 1998); allelochemical transport characterization and climate effects (Cheng, 1995; An et al., 2002); and simulation of external factors such as target plant density or fire (Weidenhamer et al., 1989; Newton and Weetman, 1994; Mallik, 2003). The development of allelochemical concentration in decomposing plant residues may be the most developed aspect in simulations of allelochemical interactions (An et al., 2002; Sinkkonen, 2003). Despite these theoretical developments, and the verified importance of allelopathy in some forest ecosystems, modelling studies that try to quantify the role of allelochemical interactions in ecosystems are scarce. Analytical models of allelochemicals in soil have generally not yet been integrated with other ecological factors in stand-level models. In this review, references to the simulation of allelopathy in forest models have only been found for FORCYTE-11 (Kimmins et al., 1990) and FORECAST (Kimmins et al., 1999). In grasslands, Goslee et al. (2001) developed improvements in the ECOTONE model to include allelochemical interactions among native and invasive species. This lack of representation of allelopathy in ecosystem models may be due to the complex mode of action of allelochemicals, which can influence processes at all levels of biological organization levels and, as a consequence, because of the lack of a comprehensive conceptual model of allelochemical interaction at the stand-level. Furthermore, there are other factors that should be taken into account in addition to the ones related to allelochemical production and toxicity. To include allelopathic relationships in ecosystem models it is neces-

sary to identify factors and effects related to allelopathy and which are coherent with the complexity of the given model.

The objective of this paper is to provide suggestions concerning the most important issues that should be taken into account when modelling allelochemical relationships in forests. A brief review of different silvicultural practices related to allelopathy which could be simulated in ecosystem management models is presented. Finally, a simulation investigation of the potential importance of allelopathy to stand growth simulation was carried out using FORECAST, an ecosystem-level forest model, to illustrate the use of allelopathy in modelling forests at an ecosystem-level.

2. The role of allelopathy in forest ecosystems

The presence of allelochemicals able to influence forest growth and development seems to be widespread in all ecosystem types. There are reports about allelochemical production in many woody species, from *Eucalyptus* sp. forests in Australia (Lovett, 1986), to boreal conifer forests (Mallik, 2003), tropical forests (McKey et al., 1978), temperate forests (Willianson et al., 1992) and sub-desert communities (Van Rooyen et al., 2004). Coder (1999) provided a detailed compilation of more than a hundred tree species with allelopathic activity. In spite of this wide distribution of allelopathic relationships, the ecological role of allelochemicals is a much-debated subject. Although it is known that allelochemicals are biomolecules produced in secondary metabolism, a controversy exists about the role of these compounds in forest ecology (Heldt, 1997), what evolutionary paths have generated allelochemical production (Reigosa et al., 1999) and even if allelopathy is a real phenomena or only a laboratory artifact (Begon et al., 1995). Perhaps the most important argument against the representation of allelopathy in ecosystem models is that reported examples of allelopathy may be explainable only in terms of competition or allelopathy acting in combination with other mechanisms (Kimmins, 2004). However, Einhellig (1995) argued that allelopathic effects cannot be considered as part of competition since they do not rely on removal of resources. Accumulated evidence hitherto shows that allelopathy may be an influential process in forest communities, where allelopathic interactions may be especially intense (Reigosa et al., 1999). Several authors think that allelopathy should be analyzed with skepticism (see Williamson (1990) for more references), because many laboratory studies are not similar to natural conditions in which allelochemicals are produced, released or affect other organisms. Furthermore, *in situ* studies of the presence and effect of allelochemicals in forest soil are very problematic, because of low concentrations, little persistence and the possibility of chemical alteration by soil microorganisms (Ma et al., 1997, Pellissier and Souto, 1999; Inderjit, 2002). Moreover, other authors argue that if plant communities have shown the capacity to adapt to herbicide application, they should have followed evolutionary paths to tolerate the presence of allelochemicals (see Reigosa et al. (1999) for further discussion of this topic). Forest modelers dealing with the situations indicated above should analyze if allelopathy may be important in their studies.

One of the uses of quantitative models in science is to integrate and summarize knowledge of a given subject (Oreskes, 2003). The inclusion of allelopathy in forest models would be a good way to analyze the potential role of this phenomenon in ecosystem dynamics, and could be a useful contribution to the controversial debates over the ecological role of allelopathy. Finally, understanding how forest ecosystems operate must involve recognition of the chemical interactions of species (Kimmins, 2004). Taking into account all of these conditions, three special cases have been mentioned as situations in which allelopathy should be analyzed: stress (Chou, 1986), invasion (Callaway, 2002) and succession (Mallik, 2003).

2.1. *Allelochemical production under stress*

Competition results when plants share limited resources. Inter-specific competition is clearly influenced by geoclimatic conditions and plants can respond using two different strategies. Firstly, plants may choose faster growth to occupy more space and, as a result, improve their chances of obtaining new resources (Grime, 1977). On the other hand, another option is to survive with lower levels of resources (Tilman, 1988). In addition to active resource competition, plants may use a passive interference in the development of their competitors by releasing allelochemicals (Reigosa et al., 2002). Taking into account that stress is any environmental condition that limits resource availability (including effects from other organisms), a positive relationship between stress intensity and allelochemical production seems logical. Chou (1989) pointed out that under severe stress that exceeds a plant's adaptive capacity, allelochemicals may act as autotoxicants, reducing the population and leaving more resources to survivor plants. Tang et al. (1995) reported that more secondary metabolites are frequently found in plants growing in nutrient-poor habitats compared to nutrient-rich sites. More evidence supporting this hypothesis was revealed by Koeppe et al. (1976), who described higher allelochemical production with phosphorus deficiency. Furthermore, the fact that some species may generate more root exudates under water stress has been tested by Kohl (1993) and Fisher et al. (1990), who reported higher allelochemical concentrations in Mediterranean shrub leaves in summer. Finally, other stress conditions that could stimulate allelochemical production are UV radiation and physical damage by herbivores (Baldwin, 1989; Reigosa et al., 1999).

2.2. *Exotic plant invasion*

Exposure to any stressful condition (such as allelochemical presence in soil), over a long period would permit the evolution of plant mechanisms by which to tolerate the stressful factor (Reigosa et al., 2002). Given that natural communities have been evolving together for centuries, Rabotnov (1974) proposed that the most important effects of allelochemicals might appear in resource competition between species which did not share a common environment in the past. This hypothesis is especially important in forestry, because allelopathy could be one of the important factors influencing the successful introduction of tree species in new regions. There

are several studies that have tested allelopathic relationships between introduced and autochthonous species (Callaway and Aschehoug, 2000; Mallik and Pellissier, 2000). The possibility of plantation failure due to allelopathy should be analyzed before introducing a new species into a forest ecosystem. Furthermore, not only should this factor be taken into account for the success of introduced trees, but also in invasions or introductions of exotic understory species that may be able to change the entire community. Recent studies have pointed out that allelochemical production and tolerance could be a key factor in determining success in exotic species invasion and in defining the new community resulting from the invasion process (Bais et al., 2003; Hierro and Callaway, 2003). In addition, Ridenour and Callaway (2001) have provided evidence that allelopathy may account for a substantial proportion of total resource interference between invasive and native plant species. Allelopathy may be an important factor to consider in certain ecosystems in order to understand the effect of individual plant species on a key ecosystem processes. Mechanistic models of soil processes can be important tools for understanding the impact of invaders, particularly if these are modified to include species dynamics (D'Antonio and Corbin, 2003).

2.3. *Succession in plant communities*

In addition to relationships between allochthonous and autochthonous species, successional processes in plant communities can be influenced by allelopathy. Phenomena such as the quick disappearance of pioneer species (Rice, 1984), long duration of intermediate phases or retrogression to secondary successional stages have been attributed to allelochemical production (Mallik et al., 1998). Moreover, understanding the role of allelopathy in succession following disturbances could be important in forest regeneration success (Rizvi et al., 1992). Most studies dealing with allelopathy in forests thus far have focused on the allelochemical influence on woody species regeneration following disturbances such as wildfires, windstorms or clearcuts (Pellissier and Souto, 1999). An excellent review by Mallik (2003) dealt with ericaceous shrub influence on conifer regeneration in Canada and northern Europe. The author noted that ericaceous shrubs proliferate during the period of higher resource availability after tree canopy removal and then allelochemical production and accumulation in forest soil increases. This is supported by the observation that conifer seedlings, the most allelochemical-susceptible stage (Einhellig et al., 1985), are not able to compete with ericaceous plants. This may be in part because their ability to develop mycorrhizae is inhibited (Inderjit and Mallik, 2002). Other studies have proven that ericaceous plant mycorrhizae are able to use allelochemicals from their host as a carbon source (Souto et al., 2000). As a result, these forests evolve into a shrubland community dominated by ericaceous plants. Only wildfires are able to reduce the presence of ericaceous shrubs and the allelochemical content in forest soil to levels which allow the successful regeneration of the tree canopy (Mallik, 2003). Changes in the mineralization and decomposition rates, as the main factors responsible for the changes in humus characteristics following a *Kalmia angustifolia* L. invasion, may be the cause of changes in soil fertility (Damman, 1971; Yamasaki et al., 1998). Similar relationships have been reported in *Cryptomeria japonica* forests in Taiwan (Chou, 1986) and in *Eucalyptus* sp. forests in Australia (Lovett, 1986).

3. Factors influencing allelochemical production by donor plants

In all stand-level models there are several factors influencing system variables and controlling the temporal evolution of those variables. In the case of allelopathy, different factors act at various points within a tree (Fig. 1). Additionally, scale is important in the modeling of allelopathy, and additional factors stand out at stand level (Fig. 2). The importance of each factor should be evaluated in each situation. Moreover, the selection of factors to be included in an ecosystem-level model should be coherent with pre-existing elements of the model in question in order to avoid unnecessary increases in model complexity and data requirements, or to allow the use of pre-existing data collections (Lauenroth et al., 2003).

3.1. *Soil factors*

Plants growing in nutrient-rich environments tend to have lower allelochemical production than plants growing on nutrient-poor sites (McKey et al., 1978; Tang et al., 1995). Water stress (caused by reduced rainfall or salinity) can increase allelochemical production (Fisher et al., 1990; Melkiana, 1992; Reigosa et al., 2002). Water soil potential determines the rate of microorganism activity, allelochemical movement and leaching (An et al., 2002). Moreover, soil texture plays an important role in the type of links between allelochemicals and soil particles. Allelochemical toxicity in arid zones with coarse texture is higher than in fine texture soils (Del Moral and Muller, 1970; Inderjit and Dakshini, 1994). Finally, Lehman et al. (1994) and Reigosa et al. (1999) pointed out the presence of herbicides, pesticides, heavy metals or other allelochemicals in the soil strongly influence allelochemical production.

3.2. *Site-specific factors*

Geographical position and climate play important roles in allelopathy. Differences in allelochemical production as a function of altitude and latitude have been reported by Anaya et al. (1992). Radiation affects donor plants, depending on wavelength, intensity and photoperiod (Koeppe et al., 1970a; Melkiana, 1992; Reigosa et al., 1999; Mallik, 2002). Temperature is another parameter affecting allelopathy. Allelochemical production increases have been reported under high temperatures (Melkiana, 1992) or under low temperatures (Koeppe et al., 1970b). Furthermore, soil temperature plays an important role in the dissipation of allelochemicals from decomposing litterfall (An et al., 2002). In addition, other local factors such as edaphic microclimate, intensity and duration of rainfall, pH or oxygen concentration may also be important (Reigosa, 1988; Weidenhamer et al., 1989; Fisher et al., 1994).

3.3. *Factors related to the donor plant*

Allelochemical production is genetically regulated, and there may be important differences in allelochemical contents

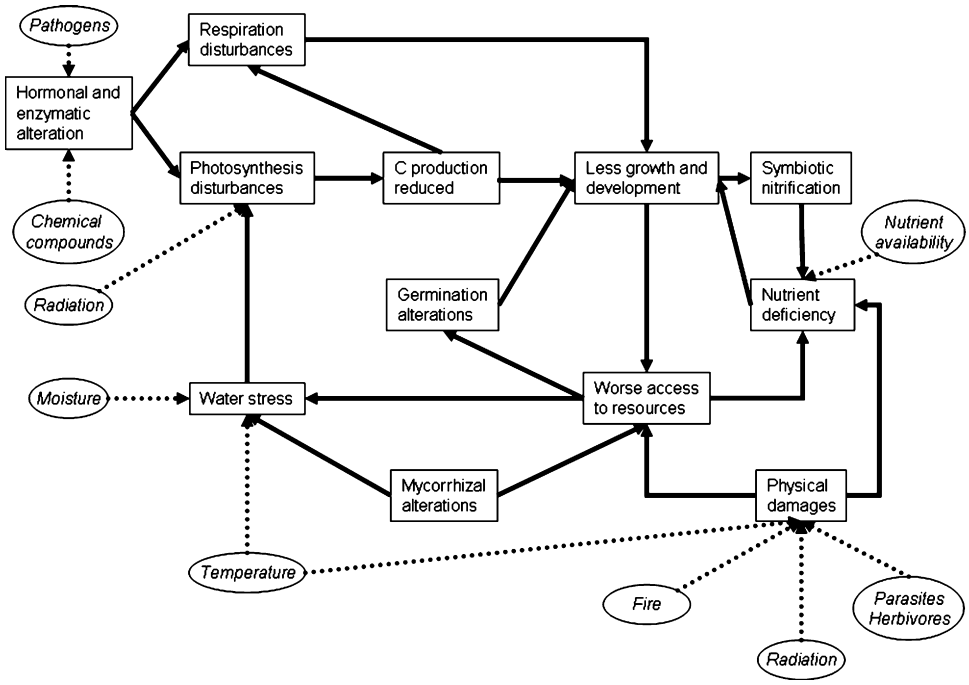

Fig. 1 – Tree-level influential factors on allelochemical production (dotted lines) and physiological effects of allelopathy (solid lines).

between donor plant genotypes (Bell and Charwood, 1980; Miller, 1996; Quader et al., 2001). A decrease in allelochemical concentration with plant age has been reported by Weston et al. (1989) and Wolfson and Murdock (1990). Pathogens, pests, parasites or herbivores can also stimulate allelochemical production (Farkas and Kiraly, 1962; Baldwin, 1989). Finally, the type of allelochemical produced by a donor plant determines its mobility in water, volatility in air, affinity to soil surfaces and degradability (Cheng, 1992; Birkett et al., 2001; Peñuelas, 2005, Fig. 2).

3.4. *Ecological factors*

Allelopathy is a phenomenon strongly related to the interaction of donor plants with their environment. In ecosystems with frequent wildfires, high production of allelochemicals by

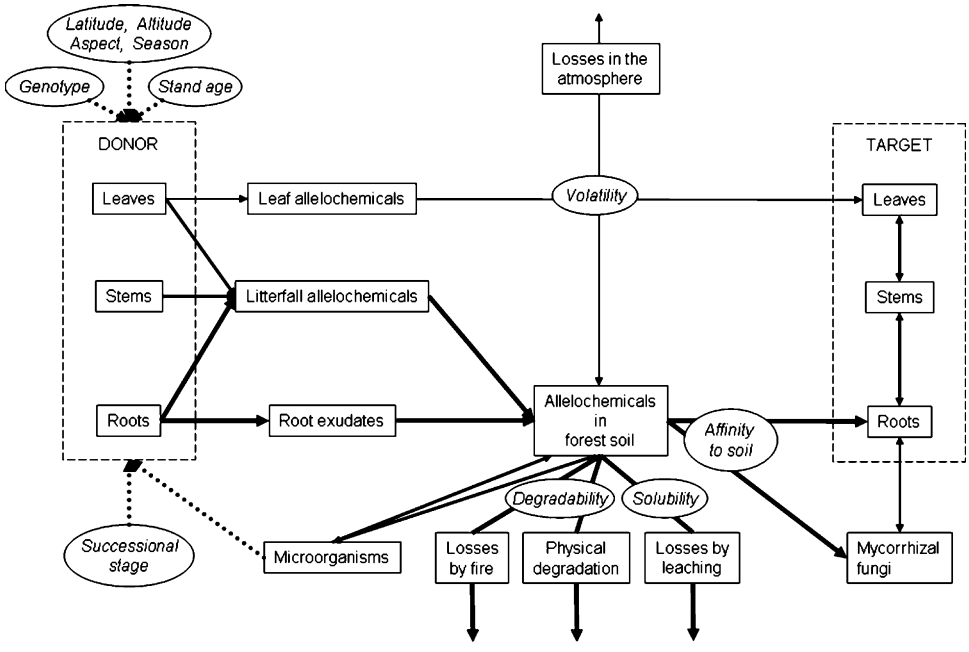

Fig. 2 – Stand-level influential factors on allelochemical toxicity (dotted lines) and transport paths of allelochemicals from donor to target plant (solid lines). Arrow thickness in solid lines is proportional to empirical evidence.

plants is observed (Williamson and Black, 1981; Coley et al., 1985). This production can be a consequence of physical damage by fire or a strategy to reduce the proliferation of highly combustible plants near the donor plant (Willianson et al., 1992). Furthermore, fire is an important factor reducing the allelochemical concentration in forest soil, via burning humus and litterfall with high concentrations of growth inhibitors (Lovett, 1986; Mallik, 2003). Other ecological factors are the presence of other organisms able to degrade allelochemicals to less toxic forms or to stimulate allelochemical production in plants (Melkiana, 1992; Reigosa et al., 1999). Target plant density is also influenced because plants growing at low densities have a larger amount of toxins available per plant to uptake (Weidenhamer et al., 1989). Finally, several studies have reported higher allelochemical production and soil concentration in late or climax successional stages (Rice and Pancholy, 1973). Nitrification in later serial stages may be strongly inhibited for this reason (Pellissier et al., 2002) and succession may be directed towards the selection of plants that inhibit nitrification of other organisms to reduce interspecific competition (Rice and Pancholy, 1973; Chou, 1986).

4. Allelopathy effects

4.1. *Tree-level effects*

Important effects of allelopathy have been identified at plant, cellular and molecular levels. For models simulating biochemical processes, such as respiration or photosynthesis, factors such as interference with hormones, enzymes or nucleic acids should be taken into account (Einhellig, 1986; Rizvi et al., 1992). At the cellular level, allelochemicals affect membrane permeability, alter chloroplast activity, chlorophyll concentration, and mitochondrial respiration rates or cause abnormal ribosome functioning, thereby reducing the efficiency of cellular function (Muller et al., 1969; Wink and Twardowski, 1992; Einhellig, 2004). These alterations reflect in plant organ function. In roots, nutrient uptake, water conductivity, nodulation or even root morphology can change because of allelochemical action (Harper and Balke, 1981; Jobidon and Thibault, 1982; Callaway, 1990; Rizvi et al., 1992). In stems, water and carbon transportation can be severely restricted (Einhellig et al., 1985). Photosynthetic efficiency and water potential in leaves are frequently altered in the presence of allelochemicals (Rizvi et al., 1992), and even seed germination ability may decrease (Wink and Twardowski, 1992; Einhellig, 2004).

4.2. *Ecosystem-level effects*

An ecosystem is the highest true level of integration in the hierarchy of ecological system complexity and it defines the key determinants of the future for the forest (Kimmins et al., 2005). The concept of allelopathy probably is more applicable to ecosystem-level processes than to population-level processes, especially in species-poor habitats where biogeochemical paths are dominated by one or two species with allelopathic proprieties (Wardle et al., 1998). Allelopathic effects at this level are directly related to forestry issues. For example, the delay and reduction of germination by allelochemicals have been widely reported (Jobidon and Thibault, 1982; Wink and Twardowski, 1992; Mallik and Pellissier, 2000). Furthermore, root development may be restricted (Muller, 1986; Mallik and Zhu, 1995), and water balance or nutrient-uptake ability impaired (Fisher, 1979), which could be the cause of important disturbances in seedling growth and development. The effects of allelochemicals on stump sprouting have been reported as well (Huang et al., 2000). In mature trees, growth stagnation by allelochemicals has been reported in mixed plantations of woody species (Rietveld et al., 1983), probably as a result of changes in water and nutrient status in mature trees (Fisher, 1979). In most severe cases, these situations lead to the death and disappearance of a species (Chou, 1986).

At the ecosystem level, not only tree plant species are affected by allelochemicals, but other organisms are also influenced. Several studies have demonstrated that allelochemicals are able to inhibit or decrease nitrification rates and affect free-living N-fixing microorganisms in forest soils (Lodhi and Killingbeck, 1980; Chou, 1986; Rice, 1992). Indirect effects of allelopathy, by altering the chemical environment in which soil microorganisms grow, could be more important to nutrient cycles than direct effects (Yamasaki et al., 1998; Inderjit and Mallik, 2002). One of the most important effects may be change in site fertility by the alteration of humus decomposition (Damman, 1971). A number of authors have attributed decreases in mycorrhizal formation to allelopathy, with dramatic consequences on tree water and nutrient uptake and consequently tree growth rates (Einhellig, 1986; Mallik and Zhu, 1995). Bacteria in forest ecosystems (free or symbiotic) may also be affected by allelochemicals (Wink and Twardowski, 1992) and, consequently, processes such as denitrification, ammonification or bacterial pathology can diminish or increase their intensity (Chou, 1986; Schmidt et al., 2000).

5. Silvicultural implications of allelopathy

Research on applied aspects of allelopathy is scarce, and most of studies focus on ways to reduce the adverse effects of allelopathy in woody species of silvicultural importance (Pellissier and Souto, 1999). Modelling is a good way to help us orient future research in this field, and the possibility of simulating the effects of techniques for dealing with allelochemicals should be integrated into stand-level models that explore the effects of silviculture in forests with allelopathic activity. The most adverse allelopathic effects have been reported in relation to the influence of the understory on tree regeneration (Mallik, 2003). The most common method of control consists of mechanical elimination of donor plants, although in some cases herbicides have been also applied (LePage et al., 1991). Another method to limit allelochemical effects is to use steam to reduce allelochemical activity (Zackrisson et al., 1997). These authors have reported an increase of *Pinus sylvestris* L. establishment and growth after using steam, especially when active carbon was added to adsorb allelochemicals. Newton and Weetman (1994) proposed high plantation densities to reach a fast canopy closure thereby reducing available energy to the understory with alle-

lochemical activity. This adverse effect on the understory could be increased by mechanical damage with mulching treatment, reduction of available energy and allelochemical autotoxicity (Pellissier and Souto, 1999). Because allelochemical effects seem to be more acute in nutrient-poor habitats, some researchers have tried to use fertilization as a method to reduce allelopathic effects. However, results obtained to date are contradictory, with a reduction in allelopathy effects after NPK fertilization (Glass, 1976; Albrektson et al., 1977; Prescott et al., 1993), and an increase in donor plants biomass following fertilization (Mallik, 1996). With the same aim to reduce adverse impacts on valuable tree species, Mallik et al. (1998) and Pellissier et al. (2002) proposed to select mycorrhizal fungi in young nursery trees that are able to resist allelochemicals and to filter these compounds before tree roots were damaged.

Forestry can also take advantage of this natural phenomenon, i.e. information about allelopathy could be used in weed control on valuable tree species, and models able to simulate allelopathic interactions could be a valuable tool in developing some of the new techniques described above. The reduction of *Rubus idaeus* L. development in *Picea mariana* (Mill.) B.S.P. forests using wheat, oat, barley or other donor plant mulching are good examples of these new techniques (Jobidon et al., 1989; Mallik, 1991). Following the same approach, Chou (1986) and Birkett et al. (2001) proposed allelopathy as a method of weed control. Finally, the ecological consequences of fire could be related to allelopathy as well. Fire is able to destroy or at least to reduce allelochemical concentrations by burning the forest soil humus layer (where most allelochemicals are stored) and helping seedlings to reach mineral soil, improving their chances to establish (Lovett, 1986). If the number and intensity of wildfires are reduced, it is possible that allelochemicals can reach levels that cause dieback in established tree species (Ellis et al., 1980) or may make tree regeneration after harvesting or windthrow almost impossible (Mallik, 2003). The effect of fire on allelopathic compounds has not been simulated hitherto in fire-related ecosystem-level models, but it could be a new approach to analyze the early development in fire-driven ecosystems with allelopathic species.

6. An example of simulation of ecosystem-level allelopathic effects with FORECAST

To our knowledge, FORECAST is the only forest ecosystem-level model specifically designed to allow the simulation of allelopathic effects. FORECAST is a stand-level, non-spatially explicit, ecosystem model. The model is based upon an approach whereby local growth and yield data are utilized to derive estimates of the rates of key ecosystem processes related to the productivity of selected species. This information is combined with data describing the rates of decomposition, nutrient cycling, light competition, and other ecosystem properties to simulate forest growth under changing management conditions. Depending on the species, plant populations are initiated from seed and (or) vegetatively, and stand development can occur with or without competition from non-target tree species and understory populations. Growth occurs in annual time steps. The driving function for potential growth of a given species is obtained by the following equation:

$$\mathrm{SCFNE}_t = \frac{\mathrm{TNPP}_t}{\mathrm{SCFN}_t} \quad (1)$$

where SCFNE_t is the shade-corrected foliar N efficiency for each annual step, TNPP_t the total primary production for each annual time step and SCFN_t is the shade-corrected foliar N content. These parameters are calculated with the following equations:

$$\mathrm{TNPP}_t = \Delta\mathrm{biomass}_t + \mathrm{ephemeral\,litterfall}_t + \mathrm{mortality}_t \quad (2)$$

where $\Delta\mathrm{biomass}_t$ = the sum of the change in mass of all the biomass components of the particular species in time step t, $\mathrm{litterfall}_t$ = the sum of the mass of all ephemeral tissues that are lost in time step t (e.g. leaf, branch, bark and reproductive litterfall, and root death), $\mathrm{mortality}_t$ = the mass of individual plants that die in time step t.

$$\mathrm{SCFN}_t = \sum_{i-1}^{n} (\mathrm{FN}_i x \mathrm{PLSC}_i) \quad (3)$$

where n = number of quarter-meter height increments in which the live canopy is divided in FORECAST, FN_i = mass of foliage nitrogen in the ith quarter-meter height increment in the live canopy and PLSC_i = photosynthetic light saturation curve value for the associated light level in the ith quarter-meter height increment in the live canopy. Data to define the production of ephemeral litterfall, tree mortality and canopy light are provided directly by field observations or derived from growth and yield tables. Decomposition is simulated using a method in which specific biomass components are transferred at the time of litterfall, to one of a series of independent litter types. These litter types decompose at rates defined by empirical data, and can be defined as measured in the presence or absence of donor plants. This model has been successfully tested against field data as a suitable management and research tool (Seely et al., 1999; Welham et al., 2002; Bi et al., in press; Blanco et al., in press). A complete detailed description of the model can be found in Kimmins et al. (1999) and it is also available online at http://www.forestry.ubc.ca/ecomodels/moddev/forecast/forecast.htm.

In this virtual experiment, I analyzed a typical situation that has been related to allelopathy in Canadian forests: the conifer regeneration problems with ericaceous understory (Mallik, 2003). The model was calibrated with data from the Research Branch of the BC's Ministry of Forests (Victoria, BC) for western redcedar (*Thuja plicata* Don.) stands in the Coastal Western Hemlock biogeoclimatic zone of the Duncan Forest District (Vancouver Forest Region, British Columbia, Canada). Four different simulations were carried out, all of them with the same starting conditions: Site index 24 m at 50 years, 3000 stems ha^{-1} as initial density, and initial aboveground biomass of salal (*Gualtheria shallon* Pursh) of 35 kg ha^{-1}. The rotation length was fixed at 100 years for all simulations. To create the starting conditions for the simulations, four 200-year rotations ending in a wildfire were simulated

(for more details about this procedure, see Kimmins et al. (1999) and Seely et al. (1999)). The first run did not simulate any allelopathic effect, and was considered a reference situation. For subsequent runs, we selected the two effects most frequently described and analyzed in the literature: a germination decrease of 15% for trees (Mallik and Pellissier, 2000), and a reduction of decomposition rates by 10% (Damman, 1971), but no micorrhizal effects were simulated in any run. Finally, the fourth run simulated both effects simultaneously. In addition, fertilization (one of the forestry practices proposed to deal with allelopathy, see above) was simulated, with the addition of 225 kg N ha^{-1} at years 22 and 40.

Results of these simulations are shown in Fig. 3. The least sensitive variable to allelopathy was dominant top height (Fig. 3), with changes lower than 3%. On the other hand, merchantable volume showed a high sensitivity to allelopathy, with changes than went beyond the levels of change in decomposition or germination rates (horizontal dashed lines) for most of the simulation period. This variable showed a clear peak in reduction after year 20 (the first year with economically valuable volume in the reference simulation), but differences between the reference and simulation of allelopathy decrease slowly but steadily after that maximum. At the end of the rotation, in the unfertilized scenario, both decomposition and germination decreased and caused a reduction of 7% in merchantable volume. When both effects are simulated simultaneously the reduction was close to 11%. A very similar pattern can be observed in the total aboveground biomass of redcedar, although in this case the reduction in biomass started more than 10 years sooner than for merchantable volume. Remarkably, the variable in FORECAST that was most sensitive to the simulation of allelopathy was salal aboveground biomass. When allelopathy was simulated as a reduction in decomposition rates, changes in salal biomass were small, but when redcedar germination was reduced (leading to a reduction in stocking to 2530 stems per hectare at the second year of the run), a significant relative increase in salal biomass was observed around year 80 (Fig. 3). Finally, it must be pointed out there was very little fertilization influence on stand response to allelopathy. For the three variables related to redcedar, results were almost identical in the fertilized and non-fertilized scenarios. The only important difference between these two scenarios was for salal aboveground biomass, with an increase of almost 150% at year 80 comparing combined simulation of allelopathy (decomposition + germination) with the reference simulation (no allelopathy).

Changes in germination and decomposition rates had opposite effects on stand development. Lower germination reduced nutrient competition between survivor trees, emulating an early self-thinning. As a consequence, it can have a positive effect on stand development and even produce taller trees in the fertilized scenario (Fig. 3). By contrast, reduction in decomposition rates caused a general reduction in stand growth. This reduction was due to lower availability of soil nutrients, which were sequestered for more time in litterfall than in the simulation without allelopathy. In addition, maximum differences caused by decomposition alteration were generally reached at the end of the rotation. However, changes in germination reduction reached the maximum differences earlier in the rotation (Fig. 3). This situation clearly points out that reduction of decomposition had a longer lasting effect on stand growth, and probably is one of the most important allelopathy effects (Damman, 1971). This effect was caused because decomposition rates were reduced by the presence of salal during the whole rotation length, while germination reduction was important only at the establishment of the new stand. In my simulation site index was little affected by allelopathic effects of salal, but merchantable volume and biomass were strongly influenced, a situation that has been commonly described in the literature (Fraser et al., 1995; Prescott and Weetman, 1994; Prescott et al., 1996). For this reason, economic and ecological analysis of stand development in situations with potential allelopathic inhibition of important species growth should consider this natural phenomenon. A final interesting result from my virtual experiment is the fact than the most sensitive variable to allelopathic simulation was the biomass of salal. My results clearly show that the ericaceous donor plant (salal) was able to take advantage of both allelopathic effects when they are simulated simultaneously, a situation in agreement with several situations reported in the literature (see Mallik (2003) for more references). Finally, it must be emphasized that fertilization had little influence in the severity of allelopathic inhibition of growth. Although immediately after fertilization a greater merchantable and aboveground biomass were reached, at the end of the rotation this positive effect was lost (Fig. 3). This was a direct consequence of an initial inhibitory effect of fertilization on salal, which caused a strong biomass decrease after fertilization, which has been previously reported in other studies (Stanek et al., 1979; Prescott et al., 1993; Bennet et al., 2004). With lower salal biomass, the total nutrient amount in the ecosystem was reduced due to higher leaching losses from the ecosystem, and, as a consequence, the available nutrients in the second part of the rotation were lower. Although more work is needed to study the utility of this practice to deal with allelopathic problems, this result agrees with Glass (1976), Albrektson et al. (1977) and Prescott et al. (1993), who reported a decrease in donor plant biomass after fertilization.

7. Conclusions

Allelopathy is a natural process likely present in all forest ecosystems and which strongly influences forest development in some cases. Conifer forests with ericaceous understory or *Eucalyptus* sp. forests are ecosystems with a strong allelopathic influence. Stress or exotic species introduction are phenomena that could increase allelopathic importance in many forests. Forest models dealing with stand-level relationships between species with confirmed allelopathic activity should include a representation of allelopathic relationships, or at least the possibility of simulating their effects in virtual experiments such this one to check model sensitivity. The ideal allelopathic model for forests would be capable of simulating the effects on tree growth of (1) Different types of disturbance—fire, plant invasion, insect outbreak, site preparation, and vegetation management. Disturbances serve to create the situation where allelopathy increases its importance for plant competition. The model should include a

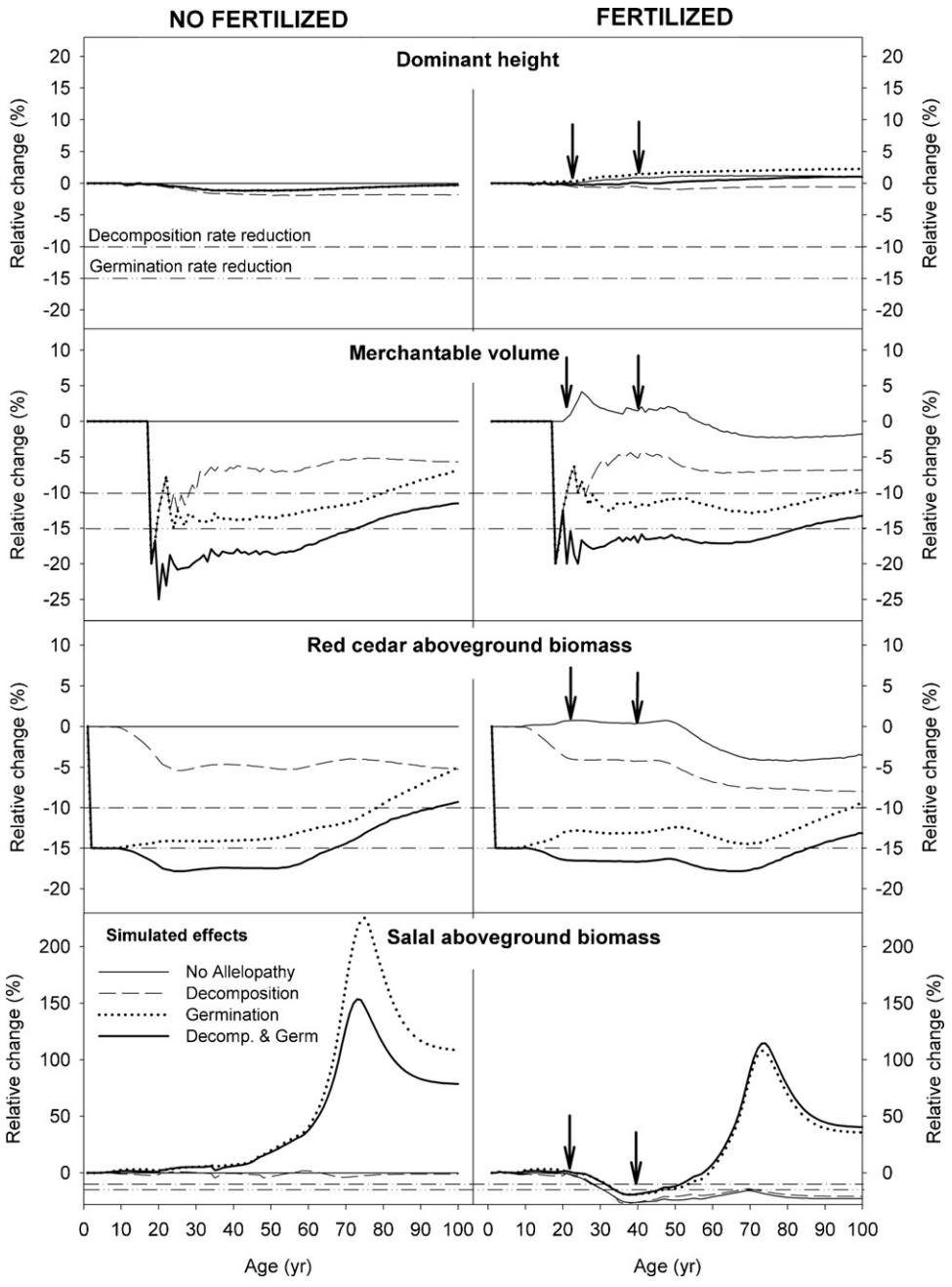

Fig. 3 – Relative differences (in %) between the simulated development of a red cedar stand in a non-fertilized scenario (reference or 0% line) and simulations of some effects of allelopathy (decomposition and germination rates reduction) in two different scenarios: Non-fertilized (left column) and fertilized with 225 kg^{-1} N ha at years 22 and 40 (right column). Arrows indicate fertilization schedule.

variation in disturbance scale, pattern and severity. (2) Seral stage, stand age, species composition, age and size class structure, slope, aspect, soil type and condition, temperature, nutrient cycling, and moisture regime. These features define the biophysical environment for allelochemical production. (3) The autoecology of tree and plant species, including allelochemical production, toxicity, dispersal, viability, and susceptibility to herbivory and pathogens, which represent the allelochemical potential of a given species. Suitable selection of factors, effects and transport paths from donor to target plants, and the biological level at which they are represented are the most important decisions to make before addressing allelopathy in forest models.

From my review, it is evident that few attempts have been made to model allelopathy at the ecosystem-level. Unfortunately, the processes involved are complex and modeling objectives vary so widely that no single approach will be sufficient. One solution is to develop a common conceptual framework from which a network of models can then be developed (Acock and Reynolds, 1990; Robinson, 1998). In this

case, the modeling objective is to devise a first approximation model which represents the beginning of a realistic analysis. Such simple models are based on first principles – cause and effect relationships – yet they can provide considerable insight (Botkin, 1993). Finally, I argue that the recommendations given above to improve ecosystem-level models for studying the effects of allelopathic interactions are also applicable to other modeling frameworks (i.e. stand- and landscape-level models). To this extent, I recognize that current scientific knowledge may be lacking in some instances, and that more extensive literature reviews (e.g. data consolidation efforts) should be undertaken before a realistic allelopathic model can be constructed. Increased data are needed for ecosystem-level models to explore the range of possibilities, rather than predict with accuracy future conditions (Welham et al., 2007). My virtual experiment has shown that the forest ecosystem-level model, FORECAST, is a suitable tool to analyze the effect of allelopathy in forest ecosystems.

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REFERENCES

Acock, B., Reynolds, J.F., 1990. Model structure and data base development. In: Rixon, R.K., Meldahl, G.A., Ruark, W.G. (Eds.), Process Modelling of Forest Growth Responses to Environmental Stress. Timber Press, Portland, Oregon, pp. 169–179.

Albrektson, A., Aronsson, A., Tamm, C.O., 1977. The effect of fertilization as primary production and nutrient cycling in the forest ecosystem. Silva Fenn. 11, 233–239.

An, M., Johnson, I.R., Lovett, J.V., 1993. Mathematical modelling of allelopathy. Biological response to allelochemicals and its interpretation. J. Chem. Ecol. 19, 2379–2388.

An, M., Johnson, I.R., Lovett, J.V., 2002. Mathematical modelling of residue allelopathy: the effects of intrinsic and extrinsic factors. Plant Soil 242, 11–22.

Anaya, A.L., Ortega, R.C., Nava Rodríguez, V., 1992. Impact of allelopathy in the traditional management of agroecosystems in Mexico. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy. Basic and Applied Aspects. Chapman & Hall, London, pp. 272–301.

Bais, H.P., Vepachedu, R., Gilroy, S., Callaway, R.M., Vivanco, J.M., 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science 301, 1377–1380.

Baldwin, I.T., 1989. Mechanism of damage-induced alkaloid production in wild tobacco. J. Chem. Ecol. 15, 1661–1680.

Begon, M., Harper, J.L., Townsend, C.R., 1995. Ecology, Individuals, Populations and Communities (Spanish translation). Blackwell Science Inc., Cambridge, p. 1050.

Bell, E.A., Charwood, B.V. (Eds.), 1980. Secondary Plant Products. Encyclopedia of Plant Physiology, vol. New Series 8. Springer, New York, p. 674.

Bennet, J.N., Lapthorne, B.M., Blevins, L.L., Prescott, C.E., 2004. Response of *Gualtheria shallon* and *Epilobium angustufolium* to large additions of nitrogen and phosphorus fertilizer. Can. J. For. Res. 34, 502–506.

Bi, J., Blanco, J.A., Kimmins, J.P., Ding, Y., Seely, B., Welham, C. Yield decline in Chinese Fir plantations: a simulation investigation with implications for model complexity. Can. J. For. Res., in press.

Birkett, M.A., Chamberlain, K., Hooper, A.M., Pickett, J.A., 2001. Does allelopathy offer real promise for practical weed management and for explaining rhizosphere interactions involving higher plants? Plant Soil 232, 31–39.

Blanco, J.A., Seely, B., Welham, C., Kimmins, J.P., Seebacher, T.M. Testing the performance of FORECAST, a forest ecosystem model, against 29 years of field data in a *Pseudotsuga menziesii* plantation. Can. J. For. Res. in press.

Botkin, D.B., 1993. Forest Dynamics: An Ecological Model. Oxford University Press, Oxford, p. 309.

Callaway, R.M., 1990. Effects of soil water distribution on the lateral root development of three species of California oaks. Am. J. Bot. 77, 1469–1475.

Callaway, R.M., 2002. The detection of neighbors by plants. Trends Ecol. Evol. 17, 104–105.

Callaway, R.M., Aschehoug, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290, 521–523.

Cheng, H.H., 1992. A conceptual framework for assessing allelochemicals in the soil environment. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy. Basic and Applied Aspects. Chapman, Hall, London, pp. 21–29.

Cheng, H.H., 1995. Characterization of the mechanisms of allelopathy, modeling and experimental approaches. In: Inderjit, Dakshini, K.M.M., Einhekkig, F.A. (Eds.), Allelopathy, Organisms, Processes and Applications. American Chemical Society, Washington, DC, pp. 132–141.

Chou, C.-H., 1986. The role of allelopathy in subtropical agroecosystems in Taiwan. In: Putnam, A.R., Tang, C.-S. (Eds.), The Science of Allelopathy. Johan Wiley & Sons, New York, pp. 57–73.

Chou, C.H., 1989. The role of allelopathy in phytochemical ecology. In: Chou, C.H., Waller, G.R. (Eds.), Phytochemical Ecology: Allelochemicals, Mycotoxins and Insect Pheromones and Allomones. Institute of Botany, Academia Sinica Monograph Series No. 9, Taipei, ROC, pp. 19–38.

Coder, K.D., 1999. Potential Allelopathy in Different Tree Species. University of Georgia, Daniel B. Warnell School of Forest Resources. pp. 1–5 (Extension publication FOR99-003).

Coley, P.D., Bryant, J.P., Chapin III, F.S., 1985. Resource availability and plant herbivore defense. Science 230, 895–899.

Damman, A.W.H., 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. Ecol. Monogr. 41, 253–270.

D'Antonio, C.M., Corbin, J.D., 2003. Effects of plant invaders on nutrient cycling: using models to explore the link between invasion and development of species effects. In: Canham, C.D., Cole, J.J., Lauenroth, W.K. (Eds.), Models in Ecosystem Science. Princeton University Press, Princeton, pp. 363–384.

Del Moral, R., Muller, C.H., 1970. The allelopathic effects of *Eucalyptus camaldulensis*. Am. Midl. Nat. 83, 254–282.

Dubey, B., Hussain, J., 2000. A model for the allelopathic effect on two competing species. Ecol. Modell. 129, 195–207.

Einhellig, F.A., 1986. Mechanisms and modes of action of allelochemicals. In: Putnam, A.R., Tang, C.-S. (Eds.), The Science of Allelopathy. Johan Wiley & Sons, New York, pp. 171–188.

Einhellig, F.A., 1995. Allelopathy: current status and future goals. In: Inderjit, Dakshini, K.M.M., Einhekkig, F.A. (Eds.), Allelopathy, Organisms, Processes and Applications. American Chemical Society, Washington, DC, pp. 1–24.

Einhellig, F.A., 2004. Mode of allelochemical action of phenolic compounds. In: Macías, F.A., Galindo, J.C.G., Molinillo, J.M.G., Gutter, H.G. (Eds.), Allelopathy, Chemistry and Mode of Action of Allelochemicals. CRC Press, Boca Ratón, p. 372.
Einhellig, F.A., Muth, M.S., Schon, M.K., 1985. Effects of allelochemicals on plant-water relationships. In: Thompson, A.C. (Ed.), The Chemistry of Allelopathy, Biochemical Interactions among Plants. American Chemical Society, Washington, DC, pp. 179–195.
Ellis, R.C., Mount, A.B., Mattay, J.P., 1980. Recovery of *Eucalyptus delegatensis* from high altitude dieback after felling and burning the understorey. Aust. Forestry J. 43, 29–35.
Farkas, G.L., Kiraly, Z., 1962. Role of phenolic compounds in the physiology of plant diseases and disease resistance. Phytopathol. Z. 44, 105–150.
Fisher, R.F., 1979. Possible allelopathic effects of reindeer-moss (*Cladonia*) on jack pine and white spruce. Forest Sci. 25, 256–260.
Fisher, N.H., Williamson, G.B., Weidenhamer, J.D., Richardson, D.R., 1994. In search of allelopathy in the Florida scrub: the role of terpenoids. J. Chem. Ecol. 20, 1355–1380.
Fisher, N.H., Weidenhamer, J.D., Riopel, J.L., Quijano, L., Menelaou, M.A., 1990. Stimulation of witchweed germination by sesquiterpene lactones: a structure–activity study. Phytochemistry 29, 2479–2483.
Fraser, L., Chanway, C.P., Turkington, R., 1995. The competitive role of *Gaultheria shallon* on planted western hemlock and western red cedar saplings on northern Vancouver Island. For. Ecol. Manage. 75, 27–39.
Glass, A.D.M., 1976. The allelopathic potential of phenolic acids associated with the rhizosphere of *Pteridium aquilinum*. Can. J. Bot. 54, 2440–2444.
Goslee, S.C., Peters, D.P.C., Beck, K.G., 2001. Modeling invasive weeds in grasslands: the role of allelopathy in *Acroptilon repens* invasion. Ecol. Model. 139, 32–45.
Grime, J.P., 1977. Evidence of the existence of three primary strategies in plants and its relevance in ecological and evolutionary theory. Am. Nat. 111, 1169–1194.
Harper, J.R., Balke, N.E., 1981. Characterization of the inhibition of K+ absorption in oat roots by salicylic acid. Plant Physiol. 68, 1349–1353.
Heldt, H.-W., 1997. Plant Biochemistry and Molecular Biology. Oxford University Press, Oxford, p. 522.
Hierro, J.H., Callaway, R.M., 2003. Allelopathy and exotic plant invasion. Plant Soil 256, 29–39.
Huang, Z., Liao, L., Wang, S., Cao, G., 2000. Allelopathy of phenolics from decomposing Stump-roots in replant Chinese fir woodland. J. Chem. Ecol. 26, 2211–2219.
Inderjit, 2002. Multifaceted approach to study allelochemicals in an ecosystem. In: Reigosa, M.J., Pedrol, N. (Eds.), Allelopathy: From Molecules to Ecosystems. Science Publishers Inc., Plymouth, pp. 271–276.
Inderjit, Dakshini, K.M.M., 1994. Allelopathic effect of *Pluchea lanceolata* (Asteraceae) on characteristics of four soils and tomato and mustard growth. Am. J. Bot. 81, 799–804.
Inderjit, Mallik, A.U., 2002. Can *Kalmia angustifolia* interference to black spruce (*Picea mariana*) be explained by allelopathy? For. Ecol. Manage. 160, 75–84.
Jobidon, R., Thibault, J.-R., 1982. Allelopathic growth inhibition of nodulated and unnodulated *Alnus crispa* seedlings by *Pupolus balsamifera*. Am. J. Bot. 69, 1213–1223.
Jobidon, R., Thibault, J.R., Fortin, J.A., 1989. Phytotoxic effect of barley, oat and wheat mulches in eastern Québec forest plantations. 1. Effects on red raspberry (*Rubus idaeus* L.). For. Ecol. Manage. 29, 277–294.
Kimmins, J.P., 2004. Forest Ecology: A Foundation for Sustainable Forest Management and Environmental Ethics in Forestry. Pearson Prentice Hall, Upper Saddle River, NJ, p. 611.
Kimmins, J.P., Mailly, D., Seely, B., 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. Ecol. Model. 122, 195–224.
Kimmins, J.P., Scoullar, K.A., Apps. M.J., 1990. FORCYTE-11 User's manual for the benchmark version. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. 294 pp.
Kimmins, J.P., Welham, C., Seely, B., Meitner, M., Rempel, R., Sullivan, T., 2005. Science in Forestry: Why does it sometimes disappoint or even fail us? Forestry Chron. 81, 723–734.
Koeppe, D.E., Rohrbaugh, L.M., Rice, E.L., Wender, S.H., 1970a. The effect of X-radiation on the concentration of scopolin and caffeoylquinic acids in tobacco. Radia. Bot. 10, 261–265.
Koeppe, D.E., Rohrbaugh, L.M., Rice, E.L., Wender, S.H., 1970b. The effect of age and chilling temperatures on the concentration of scopolin and caffeoylquinic acids in tobacco. Physiol. Plant 23, 258–266.
Koeppe, D.E., Southwick, L.M., Bittell, J.E., 1976. The relationship of tissue chlorogenic acid concentration and leaching of phenolics from sunflowers grown under varying phosphate nutrient conditions. Can. J. Bot. 54, 593–599.
Kohl, K., 1993. Allelopathy and water stress of purple nutsedge *(Luperus rotundus* L.). Master Thesis. University of Hawaii, Honolulu.
Lanchier, N., 2004. The multitype contact process with frozen states or allelopathy model. Arxiv 670 preprint math. (PR/0401353).
Lauenroth, W.K., Burke, I.C., Berry, J.K., 2003. The status of dynamic quantitative modeling in ecology. In: Canham, C.D., Cole, J.J., Lauenroth, W.K. (Eds.), Models in Ecosystem Science. Princeton University Press, Princeton, pp. 32–48.
Lehman, M.E., Blum, U., Gerig, T.M., 1994. Simultaneous effects of ferulic and *p*-coumaric acids in cucumber leaf expansion in split-root experiments. J. Chem. Ecol. 20, 1773–1782.
LePage, P., Pollack, J.C., Coates, K.D., 1991. Chemical and manual control of thimbleberry (*Rubus parviflorus*) in northwestern British Columbia: a rate and time trial. West. J. Appl. For. 6, 99–102.
Liu, D.L., An, M., Johnson, I.R., Lovett, J.V., 2003. Mathematical modeling of allelopathy. III. A Model for curve-fitting allelochemical dose responses. Nonlinearity Biol. Tox. Med. 1, 37–50.
Lodhi, M.A.K., Killingbeck, K.T., 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in a ponderosa pine *(Pinus ponderosa* Dougl.) community. Am. J. Bot. 67, 1423–1429.
Lovett, J.H., 1986. Allelopathy: the Australian experience. In: Putnam, A.R., Tang, C.-S. (Eds.), The Science of Allelopathy. John Wiley & Sons, New York, pp. 75–99.
Ma, R.X., Liu, X.F., Yuan, G.L., Sun, S., 1997. Allelochemicals and allelopathy from microorganisms in wheat rhizospheres. J. Environ. Sci. 9, 108–112.
Mallik, A.U., 1991. Cutting, burning, and mulching to control *Kalmia*: results of a greenhouse experiment. Can. J. For. Res. 21, 417–420.
Mallik, A.U., 1996. Effect of NPK fertilizations on *Kalmia angustifolia*: implications for forest disturbance and conifer regeneration. For. Ecol. Manage. 81, 135–141.
Mallik, A.U., 2002. On the question of paradigm in the science of allelopathy. In: Reigosa, M.J., Pedrol, N. (Eds.), Allelopathy: From Molecules to Ecosystems. Science Publlishers Inc., Plymouth, pp. 289–297.
Mallik, A.U., 2003. Conifer regeneration problems in boreal and temperate forest with ericaceous understory: role of disturbance, seedbed limitation, and keystone change. Crit. Rev. Plant Sci. 22, 341–366.
Mallik, A.U., Zhu, H., 1995. Overcoming allelopathic growth inhibition by micorrhizal inoculation. In: Inderjit, Dakshini, K.M.M., Einhekkig, F.A. (Eds.), Allelopathy, Organisms,

Processes and Applications. American Chemical Society, Washington, DC, pp. 39–57.
Mallik, A.U., Pellissier, F., 2000. Effects of *Vaccinium myrtillus* on spruce regeneration: testing the notion of coevolutionary significance of allelopathy. J. Chem. Ecol. 26, 2197–2207.
Mallik, A.U., Zhu, H., Park, Y.-G., 1998. Overcoming *Kalmia* induced growth in black spruce by micorrhizal inoculation. J. Kor. For. Soc. 87, 429–444.
Maynard-Smith, J., 1974. Models in Ecology. Cambridge University Press, Cambridge, p. 145.
McKey, D., Waterman, P.G., Mbi, C.N., Gartlon, J.S., Strubraker, T.T., 1978. Phenolic content of vegetation in two African rain forests: ecological implications. Science 202, 61–63.
Melkiana, N.P., 1992. Allelopathy in forest in forest and agroecosystems in the Himalayan region. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy: Basic and Applied Aspects. Chapman & Hall, London, pp. 371–388.
Miller, D.A., 1996. Allelopathy in forage crop systems. Agron. J. 88, 854–859.
Mukhopadhyay, A., Chattopadhyay, J., Tapaswi, P.K., 1998. A delay differential equations model of plankton allelopathy. Math. Biosci. 149, 167–189.
Muller, W.H., 1986. Allelochemical mechanisms in the inhibition of herbs by chaparral shrubs. In: Putnam, A.R., Tang, C.-S. (Eds.), The Science of Allelopathy. John Wiley & Sons, New York, pp. 189–199.
Muller, W.H., Lorber, P., Haley, B., Johnson, K., 1969. Volatile growth inhibitors produced by *Salvia leucophylla*: effect on oxygen uptake by mitochondrial suspensions. Bull. Torrey Bot. Club 96, 89–95.
Nakamaru, M., Iwasa, Y., 2000. Competition by allelopathy proceeds in traveling waves: colicin-immune strain aids colicin-sensitive strain. Theor. Popul. Biol. 57, 131–144.
Newton, P.F., Weetman, G.F., 1994. Stand density management diagram for managed black spruce stands. Forest. Chron. 70, 65–74.
Oreskes, N., 2003. The role of quantitative models in science. In: Canham, C.D., Cole, J.J., Lauenroth, W.K. (Eds.), Models in Ecosystem Science. Princeton University Press, Princeton, pp. 13–31.
Pellissier, F., Souto, X.C., 1999. Allelopathy in northern temperate and boreal semi-natural woodland. Crit. Rev. Plant Sci. 18, 637–652.
Pellissier, F., Gallet, C., Souto, X.C., 2002. Allelopathic interaction in forest ecosystems. In: Reigosa, M.J., Pedrol, N. (Eds.), Allelopathy: From Molecules to Ecosystems. Science Publishers Inc., Plymouth, pp. 257–269.
Peñuelas, J., 2005. Biogeoquímica y termodinámica margalefianas de los cambios globales en los ecosistemas terrestres. In: Proceedings of Unity in Diversity, a conference on ecology after the legacy of Ramón Margalef, ComoCaixa Barcelona, November 16–18, p. 29.
Prescott, C.E., Coward, L.P., Weetman, G.F., Gessel, S.P., 1993. Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*), in two coastal Douglas fir. For. Ecol. Manage. 61, 45–60.
Prescott, C.E., Weetman, G.F., 1994. Salal Cedar Hemlock Integrated Research Program: A Synthesis. Faculty of Forestry, University of British Columbia, Vancouver, BC.
Prescott, C.E., Weetman, G.F., Barker, J.E., 1996. Causes and amelioration of nutrient deficiencies in cutovers of cedar-hemlock forests in coastal British Columbia. For. Chron. 72, 293–302.
Quader, M., Daggard, G., Barrow, R., Walker, S., Sutherland, M.W., 2001. Allelopathy, DIMBOA production and genetic variability in accessions of *Triticum speltoides*. J. Chem. Ecol. 27, 747–760.
Rabotnov, T.A., 1974. On the allelopathy in the phytocenoses. Izo Akad Nauk SSR Ser. Biol. 6, 811–820.
Reigosa, M.J., 1988. Estudio del potencial alelopático de *Acacia dealbata* Link. Ph.D. Dissertation. University of Santiago de Compostela. 210 pp. (in Spanish).
Reigosa, M.J., Sánchez-Moreiras, A.M., González, L., 1999. Ecophysiological approach in allelopathy. Crit. Rev. Plant Sci. 18, 577–608.
Reigosa, M.J., Pedrol, N., Sánchez-Moreiras, A.M., González, L., 2002. Stress and allelopathy. In: Reigosa, M.J., Pedrol, N. (Eds.), Allelopathy: From Molecules to Ecosystems. Science Publlishers Inc., Plymouth, pp. 231–256.
Rice, E.L., 1984. Allelopathy, second ed. Academic Press, Orlando, p. 353.
Rice, E.L., 1992. Allelopathic effects on nitrogen cycling. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy: Basic and Applied Aspects. Chapman & Hall, London, pp. 31–58.
Rice, E.L., Pancholy, S.K., 1973. Inhibition of nitrification by climax ecosystems. II. Additional evidence and possible role of tannins. Am. J. Bot. 60, 691–702.
Ridenour, W.M., Callaway, R.M., 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126, 444–450.
Rietveld, W.J., Schelinger, R.C., Kessler, K.J., 1983. Allelopathic effects of black walnut on European black alder coplanted as a nurse species. J. Cehm. Ecol. 9, 1119–1133.
Rizvi, S.J.H., Haque, H., Sing, V.K., Rizvi, V., 1992. A discipline called allelopathy. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy: Basic and Applied Aspects. Chapman & Hall, London, pp. 1–10.
Robinson, A.P., 1998. Forest ecosystem dynamics: a systematic approach to modelling in a model-rich environment. PhD. Dissertation. University of Minnesota, 235 pp.
Schmidt, S.K., Lipson, D.A., Raab, T.K., 2000. Effects of willows (*Salix brachycarpa*) on populations of salicylate-mineralizing microorganisms in alpine soils. J. Chem. Ecol. 26, 2049–2057.
Seely, B., Kimmins, J.P., Welham, C., Scoullar, K.A., 1999. Ecosystem management models: defining stand-level sustainability, exploring stand-level stewardship. J. For. 97, 4–10.
Sinkkonen, A., 2003. A model describing chemical interference caused by decomposing residues at different density of growing plants. Plant Soil 250, 315–322.
Solé, J., García-Ladona, E., Ruardij, P., Estrada, M., 2005. Modelling allelopathy among marine algae. Ecol. Model. 183, 373–384.
Souto, C., Pellissier, F., Chiapusio, G., 2000. Allelopathic effects of humus phenolics on growth and respiration of mycorrhizal fungi. J. Chem. Ecol. 26, 2015–2023.
Stanek, W., Beddows, D., State, D., 1979. Fertilization and thinning effects on a Douglas-fir ecosystem at Shawnigan Lake on Vancouver Island. Some observations on salal and Bracken Fern undergrowth. Can. For. Ser. Pac. For. Res. Cent. Inf. Rep. BC-R-1.
Tang, C.-H., Cai, W.-F., Kohl, K., Nishimote, R.K., 1995. Plant stress and allelopathy. In: Inderjit, Dakshini, K.M.M., Einhellig, F.A. (Eds.), Allelopathy, Organisms, Processes and Applications. American Chemical Society, Washington, DC, pp. 142–157.
Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, p. 360.
Van Rooyen, M.W., Theron, G.K., van Rooyen, N., Jankowitz, W.J., Matthews, W.S., 2004. Mysterious circles in the Namib Desert: review of hypotheses on their origin. J. Arid. Env. 57, 467–485.
Wardle, D.A., Nilsson, M.-C., Gallet, C., Zackrisson, O., 1998. An ecosystem-level perspective of allelopathy. Biol. Rev. 73, 305–319.
Weidenhamer, J.D., Hartnett, D.C., Romeo, J.T., 1989. Density-dependent phytotoxicity: distinguishing resource competition and allelopathic interference in plants. J. Appl. Ecol. 26, 613–624.

Welham, C., Seely, B., Kimmins, J.P., 2002. The utility of the two-pass harvesting system: an analysis using the ecosystem simulation model FORECAST. Can. J. For. Res. 32, 1071–1079.
Welham, C., Van Rees, K., Seely, B., Kimmins, H., 2007. Projected long-term productivity in Saskatchewan hybrid poplar plantations: weed competition and fertilizer effects. Can. J. For. Res. 37, 356–370.
Weston, L.A., Harmon, R., Mueller, S., 1989. Allelopathic potential of sorghum–sudangrass hybrid (sudex). J. Chem. Ecol. 15, 1855–1865.
Williamson, G.B., 1990. Allelopathy, Koch's postulates, and the Neck Ridle. In: Grace, J.B., Tilman, D. (Eds.), Perspectives on Plant Competition. Academic Press, San Diego, pp. 143–162.
Williamson, G.B., Black, E.M., 1981. High temperature forest fires under pines as a selective advantage over oaks. Nature 293, 634–644.
Willianson, G.B., Richardson, D.R., Fischer, N.H., 1992. Allelopathic mechanism in fire-prone communities. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy: Basic and Applied Aspects. Chapman & Hall, London, pp. 57–75.
Wink, M., Twardowski, T., 1992. Allelochemical properties of alkaloids. Effects on plants, bacteria and protein biosynthesis. In: Rizvi, S.J.H., Rizvi, V. (Eds.), Allelopathy: Basic and Applied Aspects. Chapman & Hall, London, pp. 129–150.
Wolfson, J.L., Murdock, L.L., 1990. Growth of *Manduca sexta* on wounded tomato plants: role of induced proteinase inhibitors. Entomol. Exp. Appl. 54, 257–264.
Yamasaki, S.H., Fyles, J.W., Egger, K.H., Titus, B.D., 1998. The effect of *Kalmia angustifolia* on the growth, nutrition, and ectomycorrhizal symbiont community of black spruce. For. Ecol. Manage. 105, 197–207.
Zackrisson, O., Norberg, G., Dolling, A., Nilsson, M.C., Jäderlund, A., 1997. Site preparation by steam treatment: effects on forest vegetation control and establishment, nutrition, and growth of seeded Scots pine. Can. J. For. Res. 27, 315–322.